INHERITANCE OF RESISTANCE TO BUNT, *TILLETIA TRITICI* (BJERK.) WINTER, AND OTHER CHARACTERS IN CERTAIN CROSSES OF "FLORENCE" WHEAT.

By J. G. Churchward, B.Sc.Agr. (Syd.),
Walter and Eliza Hall Agriculture Research Fellow, University of Sydney.

(Four Text-figures.)

[Read 25th May, 1932.]

Introduction.

Severe losses are occasioned by Bunt or Stinking Smut in wheat crops throughout the world. The losses are due to reduction in yield and to depreciation in the quality and market value of the grain.

In certain of the United States of America heavy losses occur annually, particularly in the winter wheats. The heavy infection is largely due to the wind-blown spores which lead to "soil infection" of the crop. The position in Australia is different. Here "Spring" habit wheats, sown in April-May, grow during the comparatively mild winter weather and are harvested in November-December. Soil infection seldom occurs under these conditions.

In England, largely owing to the moist seed-bed conditions at sowing time, steeping the grain in formalin is found to prevent bunt. In Australia the dry copper carbonate treatment is most effective. It was pointed out in a previous paper (Churchward, 1931) that this method is costly and acts as a preventive and not as a cure. Even so, considerable areas are sown every year with untreated grain. In the 1931 season, when crops were considered to be particularly clean, bunted samples from many districts of all the States of Australia were received.* The solution of the problem seems to lie in making use of the inherent qualities of resistance to bunt, possessed by some varieties, in developing types of commercial value that will resist attacks of the causal fungus.

It is unnecessary to stress the importance of knowing the manner in which the resistance of certain varieties is inherited. There are no commercial Australian wheats that are immune to bunt. "Florence", one of the Farrer varieties, is one of our most resistant wheats, and this quality marks it as a valuable parent for breeding work. A knowledge of its genetical behaviour is therefore desirable.

Review of Literature.

Farrer (1901) was the first worker to breed wheats specifically for bunt resistance. He produced two varieties, "Florence" and "Genoa", which gave low percentages of bunt (Pye, 1909). This "Florence" is the resistant parent used in the work herein described.

In 1905 Biffen showed that resistance to yellow rust (*Puccinia glumarum* Erikss.) behaves as a simple Mendelian recessive character. Since that time

---

* A further paper will deal with the distribution of the species of *Tilletia* in Australia.

ability to resist many other diseases has been found to be inherited in a Mendelian fashion.

Gaines (1920) was the first worker to record the mode of inheritance of resistance to bunt of wheat. He considered that resistance, if inherited on Mendelian lines, was due to multiple factors. Varieties possessed different kinds of resistance, and the factors varied in their potency. For example, the factor carried by "Turkey" was supposed to be four times as powerful as that carried by "Marquis" (Gaines and Singleton, 1926). He claimed (1925) that some varieties have no heritable factors for resistance; others have two or three cumulative factors, each reducing the amount of bunt by 10–15 per cent. The factors may be concentrated by crossing (Gaines, 1923). "Florence" was supposed to possess several factors which reduce the amount of bunt by 70–75 per cent. when compared with susceptible varieties. In crosses between immune and susceptible varieties, resistance was found to be dominant. When a resistant variety like "Florence" was crossed with a susceptible variety, dominance of susceptibility resulted.

Briggs (1926) showed that there was a single factor difference for resistance between "Martin" and "Hard Federation". His results indicated that susceptible varieties possessed no factors for resistance. He demonstrated (Briggs, 1926) that "Hussar" differs from susceptible varieties such as "Baart" by two factors, one being identical with that possessed by "Martin", the other allowing the development of bunt in 50 per cent. of the heterozygous families. Further investigations (Briggs, 1929; 1931) showed that "White Odessa" and "Banner Berkeley" wheats differed from "White Federation" by one factor for resistance. This factor was identical with the one carried by "Martin". Briggs (1929) further found that modifying factors may influence the resistance of a variety to bunt. In a cross between "Hussar" (resistant) and "Hard Federation" (susceptible), strains were isolated which bred true for a small percentage of bunt infection.

In Australia, the writer (Churchward, 1931) showed that there was a single factor difference between "Florence" and "Hard Federation".

Material and Methods.

The various crosses were made in 1927 at the University of Sydney. The F_1 generations were grown in 1928, each F_1 plant being harvested separately. This generation was not inoculated. Portion of the harvest was kept; the other part was sown, uninoculated, and harvested as F_2 plants in 1929. In this way F_2 and F_3 grain of a single cross was available for sowing at one time—both generations being subjected to the same environmental conditions.*

In late June, 1931, the F_2 and F_3 generations were sown at Hawkesbury Agricultural College, Richmond, N.S.W., in a light red loam, of good depth, well aerated and drained, with an acid reaction. The sowing of the block of "Florence" crosses was completed within five days in order to minimize any effects from changing conditions within the soil.

The grain was inoculated with fresh spores of *Tilletia tritici* just before planting. The seed was shaken with an excess of inoculum in a test-tube until thoroughly blackened. The excess of bunt was tipped into the packet with the seeds.

The inoculum was originally obtained from Dr. W. L. Waterhouse in 1927. Since then it has been grown annually on "Federation" or "Hard Federation". All crosses were treated with this same inoculum.

---

* Material was kindly supplied by Dr. W. L. Waterhouse of the Sydney University.

The grains were sown by hand half a link apart in 15-link rows. The rows were two links apart.

During the period of growth of the crop the occurrence of dwarfs or grass clumps was noted. The habit and dates of maturity in F_2 and F_3 generations of several crosses were studied.

Each plant was harvested separately and placed in one of three groups: (1) Bunt free, (2) plants showing "late tiller" infection, (3) Bunted. "Florence" showed approximately 18% "late tiller" infection. This type of infection was regarded as resistance.

Gaines (1923) made a quantitative estimate of the bunt present in each row. Briggs (1926) pointed out that, although this method gives a satisfactory quantitative measure of infection, the nature of the segregation is not indicated, as each plant ceases to be regarded as a genetical identity.

Parent Stock.

The varieties discussed in this paper are all common wheats (*Triticum vulgare*, Host.) having commercial importance. Their main characteristics are as follows:

"Florence" is an early-maturing variety, with a light-chaffed ear which is tip-awned. It shatters badly when being harvested, much grain being lost. It is notably resistant to bunt.

The remaining five varieties are susceptible to bunt: "Yandilla King" is the standard late-maturing variety in New South Wales. It is one of the heaviest yielders and is the most popular of the late varieties, being the third leading variety in the State. The young growth is prostrate in habit. "Marshall's No. 3" ranks second in popularity amongst the late wheats. It is a heavy yielder and the eighth leading variety in New South Wales. It has a purple pigment in the straw. "Firbank" is a very early maturing wheat. "Gullen" is an early variety with brown tapering ears. The grain is included in the strong flour type. It holds the grain well. "Hard Federation" is an early mid-season wheat. The brown ear is bald.

Experimental Results.

Segregation in F_2 Generation.

The percentage of infection obtained in the F_2 generations and parent controls is recorded in Table 1.

Table 1.—Bunt infection obtained in varieties and F_2 generations.

Parents or Cross.	No. of Plants.		Percentage of Susceptible Plants.
	Totals.	Susceptible.	
Florence	940	65	6·5
Firbank	913	706	77·3
Gullen	337	267	79·2
Yandilla King	278	212	76·3
Marshall's No. 3	293	257	88
Florence × Firbank	546	369	67·6
Gullen × Florence	444	309	69·6
Florence × Yandilla King	310	169	54·5
Marshall's No. 3 × Florence	54	24	45

It will be seen that susceptibility is dominant.

The percentage of infection shown by the susceptible parents indicates that some plants in susceptible varieties escape infection. It is assumed that enough F_2 susceptible plants escaped infection to bring the percentage of infection up to 75 per cent. This assumption is confirmed by the F_3 results. On this basis "Florence" would seem to differ from each of the four susceptible parents by a single recessive factor for resistance to bunt.

The comparatively low percentage of bunt infection in the "Marshall's No. 3" × "Florence" cross cannot be regarded as significant. A poor germination in the F_2 gave a small number of plants. The F_3 showed normal segregation on monohybrid lines.

Segregation in F_3 Generation.

A number of F_3 families of each of the crosses were taken at random and the inoculated grain was sown. The grain was derived from the untreated portion of the F_2 generation sown in 1929. Thus susceptible families were grown which would have been lost in the F_2 generation, as totally smutted plants become automatically eliminated.

Further, while some susceptible plants in the F_2 generation may escape infection, it is not probable that an entire F_3 row will escape. The F_3 generation results are clearly more reliable than are the F_2.

"Florence" × "Firbank".

The reciprocal of this cross was used. As there was no difference in the type of reaction, the results of both crosses were combined. In this series there were 270 families represented, with check rows of each parent every tenth row. F_3 data are recorded in Table 2.

TABLE 2.—Distribution of parent and F_3 rows of the cross, "Florence" × "Firbank", into 5 per cent. classes for bunt infection.

Parents and Cross.	Distribution of Rows by Percentage Classes for Bunt Infection.																				No. of Rows
	0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	
Florence ..	23	—	8	3	1																	35
Firbank ..											1	—	2	—	6	5	5	7	5	3	1	35
Florence × Firbank ..	20	3	13	23	12	15	17	20	21	26	19	12	9	12	16	11	8	5	3	2	3	270

The average infection of the "Florence" controls was 3·4 per cent., the spread being over 4 classes. There were 75 per cent. of the "Firbank" controls bunted, ranging from the 46–100 per cent. class. The nature of the distribution is seen in Figure 1.

The broken line joining the plotted points makes an irregular graph. This is due to the comparatively small numbers of families in the various F_3 generations, and further to the small number of plants in each family (average = 20 plants). In other words, in a single family, the addition or subtraction of one plant would be equivalent to a change of 5 per cent. on the average, for susceptibility or resistance. As the range of the classes for bunt infection is 5 per cent., the probability of a family being incorrectly classed is fairly great. The continuous line is a smooth curve through these points and is probably a truer graphic interpretation of the figures given in Table 2.

The formation of a trimodal curve indicates a 1:2:1 ratio. The first minimum lies at 17·5 per cent. infection, and the second at 57·5 per cent. These do not strictly divide the homozygous and heterozygous genotypes. A certain amount of overlapping of the individuals is to be expected. At the lower minimum the balance lies slightly in favour of the heterozygous class, while at the higher minimum it favours the homozygous class. The numbers at these minima, however, are so small that they do not materially interfere with the counts. Sixty-five homozygous resistant families were obtained where 67·5 were expected, 136 heterozygous families where 135 were expected, and 69 homozygous susceptibles where 67·5 were expected. This closely approximates a 1:2:1 ratio, thus confirming the F_2 results.

A single factor difference for resistance to bunt, with dominance of susceptibility, is indicated in the cross between "Florence" and "Firbank".

"*Gullen*" × "*Florence*".

In this series there were 106 families with check rows of both parents distributed every tenth row. F_3 data are recorded in Table 3.

TABLE 3.—Distribution of parent and F_3 rows of the cross, "Gullen" × "Florence", into 5 per cent. classes for bunt infection.

Parents and Cross.	Distribution of Rows by Percentage Classes for Bunt Infection.																					No. of Rows.
	0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	
Florence ..	3	2	—	3	1	2																11
Gullen ..													1	—	4	—	3	—	6	1	—	15
Gullen × Florence ..	12	—	2	3	6	6	2	7	9	10	13	5	6	1	6	8	5	2	2	—	1	106

The average infection of the "Florence" controls was 13 per cent., and that of "Gullen" 79·2 per cent. The nature of the distribution is seen in Fig. 2. In this case the two minima lie at 27·5 per cent. and 62·5 per cent. respectively. The number of plants lying between the minima is shown in Table 4.

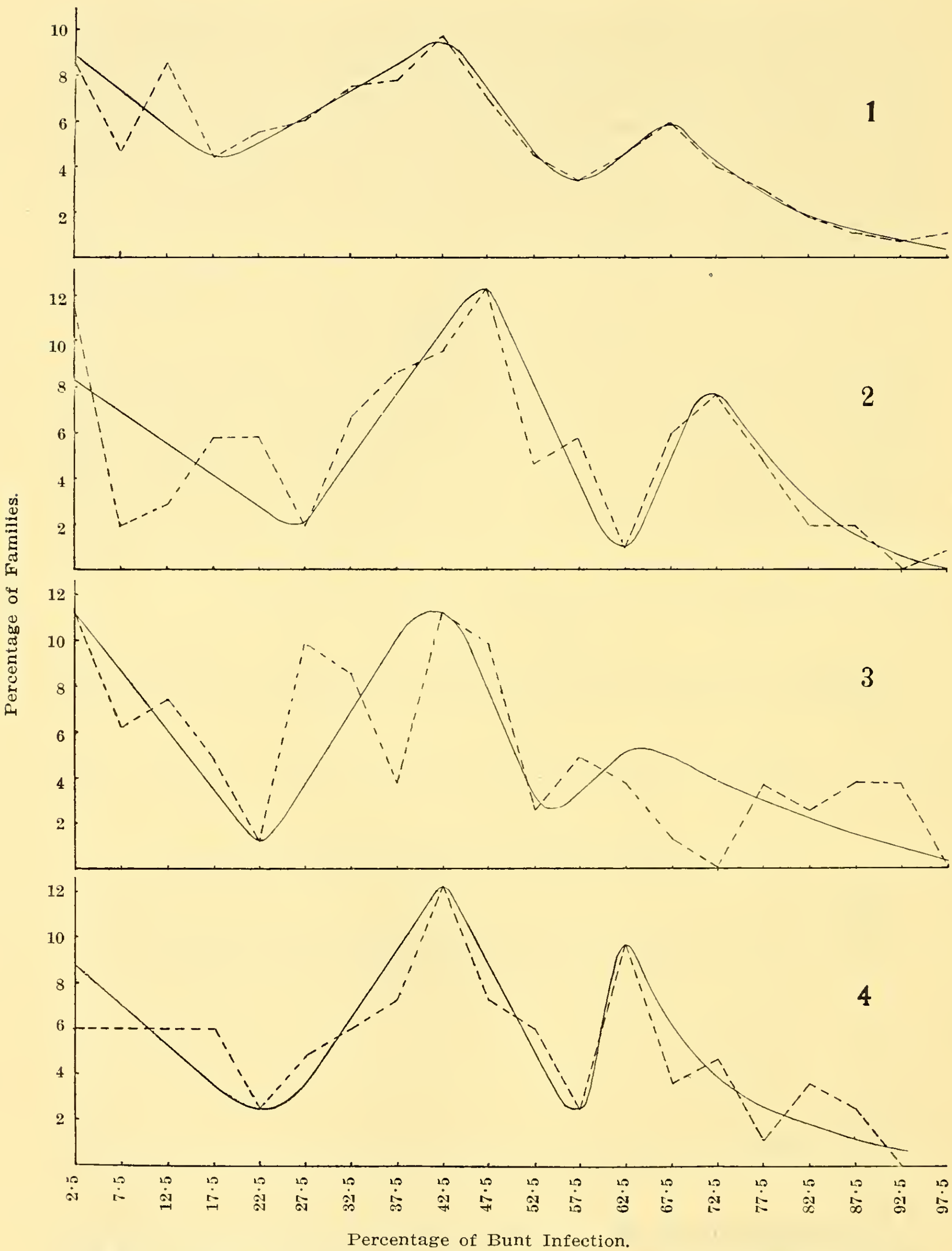

Fig. 1.—Distribution of F_3 families of the cross, "Florence" × "Firbank", in 5 per cent. classes for bunt infection.

Fig. 2.—Distribution of F_3 families of the cross, "Gullen" × "Florence", in 5 per cent. classes for bunt infection.

Fig. 3.—Distribution of F_3 families of the cross, "Florence" × "Yandilla King", in 5 per cent. classes for bunt infection.

Fig. 4.—Distribution of F_3 families of the cross, "Marshall's No. 3" × "Florence", in 5 per cent. classes for bunt infection.

TABLE 4.—Classification of families in the F_3 generation of a cross, "Gullen" × "Florence".

Kind of Family.	No. of Families.	
	Observed.	Expected.
Homozygous Resistant	30	26·5
Heterozygous	51	53
Homozygous Susceptible	25	26·5
Totals	106	106

There is, therefore, a close approximation to a 1:2:1 ratio. There are 76 susceptible families compared with 30 resistant to bunt. The P.E. for a 3:1 ratio in a population of 106 is 3·01, and $\frac{D.}{P.E.} = 1{\cdot}2$. There is a single factor difference between "Gullen" and "Florence" for bunt resistance, with dominance of susceptibility.

"Florence" × "Yandilla King".

The number of families grown in the F_3 of this cross was small. Eighty-one rows were sown with parent checks planted every 10 rows. Results are tabulated as follows:

TABLE 5.—Distribution of the parent and F_3 rows of a cross, "Florence" × "Yandilla King", into 5 per cent. classes for bunt infection.

Parents and Cross.	Distribution of Rows by Percentage Classes for Bunt Infection.																					No. of Rows
	0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	
Florence ..	3	1	1	2	1																	8
Yandilla King														1	1	4	—	6	—	—	—	12
Florence × Yandilla King	6	3	5	6	4	1	8	7	3	9	8	2	4	3	1	—	3	2	3	3	—	81

The average infection of the "Florence" controls was 8·7 per cent., and the "Yandilla King" controls 76·3 per cent. The nature of the distribution is seen in Fig. 3. The two minima lie at 22·5 per cent. and 52·5 per cent. The number of plants lying between the minima is shown in Table 6.

TABLE 6.—Classification of families in the F_3 generation of a cross, "Florence" × "Yandilla King".

Kind of Family.	No. of Families. Observed.	No. of Families. Expected.
Homozygous Resistant	24	20·25
Heterozygous	38	40·5
Homozygous Susceptible	19	20·25
Totals	81	81

This approximates a 1:2:1 ratio. There are 57 susceptible families compared with 24 resistant to bunt. The P.E. on a 3:1 expectancy in this population is 2·63, and $\frac{\text{D.}}{\text{P.E.}} = 1{\cdot}5$. The results indicate a single factor difference between "Florence" and "Yandilla King" for bunt resistance, with dominance of susceptibility.

"Marshall's No. 3" × "Florence".

Again the number of the F_3 families grown was small, but sufficient to indicate the mode of inheritance. Eighty-three rows were sown, with parental controls every tenth row. Results are recorded in Table 7.

TABLE 7.—Distribution of parent and F_3 rows of a cross, "Marshall's No. 3" × "Florence", into 5 per cent. classes for bunt infection.

Parents and Cross.	Distribution of Rows by Percentage Classes for Bunt Infection. 0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	No. of Rows.
Florence ..	4	2	3	1	1																	11
Marshall's No. 3 ..																1	—	2	5	3	1	12
Marshall's No. 3 × Florence ..	5	—	5	5	5	2	4	5	6	11	6	5	2	8	3	4	1	3	2	—	—	83

The "Florence" controls showed 6 per cent. infection and the "Marshall's No. 3" controls 87 per cent. The nature of the distribution is seen in Fig. 4. The minima lie at 22·5 per cent. and 57·5 per cent. These separate the F_3 families into three types as shown in Table 8.

TABLE 8.—Classification of families in the F_3 generation of a cross, "Marshall's No. 3" × "Florence".

Kind of Family.	No. of Families.	
	Observed.	Expected.
Homozygous Resistant	21	20·75
Heterozygous	40	41·5
Homozygous Susceptible	22	20·75
Totals	83	83

This is a close approximation to a 1:2:1 ratio. There is no significant deviation from the expected results. This indicates a single factor difference between "Marshall's No. 3" and "Florence" for bunt resistance, with dominance of susceptibility.

Grass Clumps.

Many workers have noted the occurrence of dwarf plants or grass clumps in segregating generations of wheat crosses. They occur also in barley, oat, and rye crosses. Waterhouse (1930) records the results of a number of crosses, the majority of which, in F_2, gave a ratio of 13 normals : 3 grass clumps, indicating the action of inhibiting factors. A few gave 15 normal plants : 1 grass clump.

Five of the crosses under consideration showed segregation for grass clumps in the F_2 generation. Four of them segregated as follows:

TABLE 9.—Occurrence of grass clumps in the F_2 generation of certain wheat crosses on a 13 : 3 expectancy.

Parents of Cross.	Observed.			Expected.		$\frac{D.}{P.E.}$
	Totals.	Normals.	Grass Clumps.	Normals.	Grass Clumps.	
Gullen × Florence	232	187	45	189	43	$\frac{2}{4\cdot01}=0\cdot49$
Florence × Gullen	326	264	62	265	61	$\frac{1}{4\cdot75}=0\cdot21$
Marshall's No. 3 × Florence..	72	58	14	58·5	13·5	$\frac{0\cdot5}{2\cdot23}=0\cdot22$
Roseworthy × Florence ..	249	201	48	202	47	$\frac{1}{4\cdot15}=0\cdot24$

The nature of the segregation in the F_2 generation of these crosses indicates the presence of an inhibiting factor. The F_3 families of all crosses except "Florence" × "Gullen" were grown in 1931. An analysis of these families gives the following results:

TABLE 10.—Number of F_3 families segregating for grass clumps compared with families producing only normals on a 6 : 7 expectancy.

Parents of Cross.	Phenotype.	No. of Families.		$\frac{D.}{P.E.}$
		Observed.	Expected.	
Gullen × Florence	Normal Segregating	53 52	56 49	$\frac{3}{3 \cdot 44} = 0 \cdot 87$
Marshall's No. 3 × Florence	Normal Segregating	42 41	44 39	$\frac{2}{3 \cdot 06} = 0 \cdot 65$
Roseworthy × Florence	Normal Segregating	41 29	37 33	$\frac{4}{2 \cdot 81} = 1 \cdot 42$

The Probable Error for various populations for the ratio 6:7 was calculated from the formula $E.P._n = \pm\ 0 \cdot 6745 \sqrt{pqn}$ (Hayes and Garber, 1927).

The results confirm the F_2 assumption of the presence of an inhibiting factor for dwarfness.

Different results were obtained in the cross "Florence" × "Yandilla King".

In the F_2, the count for grass clumps showed 313 normal plants : 44 dwarfs. This approximates to a 55:9 ratio and indicates the presence of a dominant inhibiting factor and two dominant factors for dwarfness. Waldron (1924) obtained an approximation to this ratio in a "Kota" × "Marquis" cross.

TABLE 11.—Number of normal plants compared with number of grass clumps in F_2 generation of a cross, "Florence" × "Yandilla King", on a 55 : 9 expectancy.

Kind of Plant.	No. of Plants.		$\frac{D.}{P.E.}$
	Observed.	Expected.	
Normals	313	308	$\frac{5}{4 \cdot 43} = 1 \cdot 1$
Grass Clumps	44	49	
Totals	357	357	

The Probable Errors of the Mendelian ratios 55:9 and 37:18 were calculated from the formula $E.P._n = \pm\ 0 \cdot 6745 \sqrt{pqn.}$

This result closely approximates to the expectancy.

Counts were made in the F_3 generation for families producing only normal plants, and families segregating for the grass clump habit. They were as follows:

TABLE 12.—Number of F_2 families segregating for grass clumps compared with number of families producing only normals in a cross, "Florence" × "Yandilla King", on 18 : 37 expectancy.

Phenotype of F_3 Family.	No. of Families.		$\frac{D.}{P.E.}$
	Observed.	Expected.	
Segregating..	52	54	$\frac{2}{2\cdot85}=0\cdot7$
Non-Segregating	29	27	
Totals	81	81	

This is a close approximation to the expected results and confirms the F_3 assumption.

Chaff Colour.

The inheritance of chaff colour has been studied by many workers. Biffen (1905), Kezer and Boyack (1918) and others obtained F_1 plants of intermediate colour and 3:1 segregation for coloured : colourless chaff in the F_2 generations.

In Australia Waterhouse (1930) obtained ratios approximating to 3 coloured: 1 white chaff plant in the segregating generations of certain crosses.

"Gullen" × "Florence".

Segregation for chaff colour in the F_2 and F_3 generations of the cross between "Gullen" (brown chaff) and "Florence" (light chaff) was studied. The F_1 was intermediate in colour. Results of F_2 are shown in Table 13.

TABLE 13.—Classification of F_2 plants for chaff colour and resistance to bunt in a cross, "Gullen" × "Florence", on 9 : 3 : 3 : 1 expectancy.

Number of Plants.	Brown-Chaffed.		White-Chaffed.	
	Susceptible.	Resistant.	Susceptible.	Resistant.
Observed	227	101	82	34
Adjusted	244	84	88	28
Expected	249·75	83·25	83·25	27·75
$\frac{\text{Deviation}}{\text{Probable Error}}$	$\frac{5\cdot75}{7\cdot05}=0\cdot8$	$\frac{0\cdot75}{5\cdot55}=0\cdot1$	$\frac{4\cdot75}{5\cdot55}=0\cdot8$	$\frac{0\cdot25}{3\cdot42}=0\cdot1$

There were 328 brown-chaffed plants and 116 white-chaffed. The P.E. for this population on a 3:1 expectancy is 6·15. $\frac{D.}{P.E.} = 0{\cdot}81$. Approximately 7·2 per cent. of the susceptible F_2 plants in this cross escaped infection. Assuming that all susceptible plants had become infected, the numbers of plants in each class were calculated. The adjusted figures give a close approximation to a 9:3:3:1 ratio.

There does not appear to be any correlation between inheritance of chaff colour and resistance to bunt.

Results of the F_3 of the cross grown in the same year are shown in Table 14.

TABLE 14.—Classification of families for chaff colour in the F_3 of a cross, "Gullen" × "Florence", on a 1 : 2 : 1 expectancy.

Chaff Colour.	No. of Families.	
	Observed.	Expected.
Homozygous brown	23	26·5
Heterozygous brown	56	53
Homozygous white	27	26·5
Totals	106	106

There were 89 families with brown chaff and 27 with white chaff. The P.E. for this population on a 3:1 expectancy is 3·01, and $\frac{D.}{P.E.} = 0{\cdot}16$. This is a very close approximation to the expectancy, and indicates a single dominant factor for chaff colour in the cross.

"Hard Federation" × "Florence".

The F_1 of a cross between "Hard Federation" (brown chaff) and "Florence" (white) was intermediate in colour. In the F_2 the chaff of plants was classed as brown or white. There were 201 brown-chaffed plants where 196 were expected, and 60 white-chaffed plants where 65 were expected. The P.E. for this population on a 3:1 expectancy is 4·75, and $\frac{D.}{P.E.} = 1{\cdot}0$. The results indicate a single factor difference for chaff colour between "Hard Federation" and "Florence". Results in the F_3 confirm this.

The P.E. for a population of 223 on a 3:1 expectancy is 4·36, and $\frac{D.}{P.E.} = 0{\cdot}4$.

Fifteen F_4 rows were sown at Richmond in 1930 with inoculated grain. The seed was selected at random from F_3 families heterozygous for chaff colour. A study of the resulting infection indicated that there was no correlation between the inheritance of chaff colour and resistance to bunt.

TABLE 15.—Classification of families for chaff colour in the F_3 of a cross, "Hard Federation" × "Florence", on 1 : 2 : 1 expectancy.

Chaff Colour.	No. of Families.	
	Observed.	Expected.
Homozygous brown	51	55·75
Heterozygous brown	118	111·5
Homozygous white	54	55·75
Totals	223	223

DISCUSSION.

In the present work, "Florence" was crossed with four susceptible commercial Australian varieties of wheat. Each cross gave a similar result. A graph, representing the distribution of F_3 families in 5 per cent. classes for bunt infection, showed a trimodal curve in each case, indicating a single factor difference for bunt resistance.

In such types of Mendelian inheritance, heterozygous F_3 families segregate in the same manner as the F_2 generation. The F_3 heterozygous families in these studies did not average the 75 per cent. of bunted plants as was expected. An average of 42 per cent. was obtained.

This low percentage would seem to be due to the following: (1) The number of families and the number of plants in each family were comparatively low (av. = 20 plants). Remnants of the F_2 plants were kept for further inoculation studies with flag-smut, so that only a portion of the grain from each F_2 plant was available for the bunt tests. (2) Environmental conditions were such that a certain percentage of the susceptible plants escaped infection. In consequence the true behaviour of all the heterozygous plants was not demonstrated.

The results emphasize the necessity of having complete control of the environmental conditions, so that all susceptible plants may become infected.

The phenotypes in the "Florence" crosses were separated by the two minima on the assumption that the amount of overlapping of the heterozygous and homozygous families was equal.

"Florence" is resistant, but not immune, to bunt. Low percentages of infection may be due to factors which modify resistance (Briggs, 1929*c*). Gaines (1920) suggested that some varieties possessed the ability to retard the growth of the fungus. It is generally believed that "Florence" owes its resistance to its ability to grow away from the fungus.

Under field conditions, "Florence" would be expected to produce, on the average, less than 2 ears per plant (Forster and Vasey, 1931). In the experimental plots, the average number of ears produced was 3·4 per plant. This was mainly due to the grains being planted at 4-inch intervals in drills 2 links apart. Some of the late "tillers" of "Florence" became infected. These tillers would not have been produced under ordinary conditions. This "late-tiller" infection was regarded as resistance.

Summary.

In a previous paper, the inheritance of resistance to bunt in a cross "Florence" × "Hard Federation" was studied. The data showed a single factor difference with dominance of susceptibility.

For these studies "Florence" was crossed with four susceptible commercial Australian varieties, namely, "Firbank", "Gullen", "Yandilla King" and "Marshall's No. 3".

The F_2 and F_3 generations derived from single F_1 plants were grown in 1931. Each cross gave similar results.

In the F_3 generation, the three classes, homozygous susceptible, heterozygous susceptible, and homozygous resistant, gave a close approximation to a 1:2:1 ratio. The results indicated a single factor difference with dominance of susceptibility, between "Florence" and each of the four susceptible varieties.

The occurrence of grass clumps in the progeny of the crosses was studied. Three of the crosses gave ratios of 13 normals : 3 grass clumps, indicating the action of an inhibiting factor. In the cross "Florence" × "Yandilla King", the F_2 counts approximated to a 55:9 ratio. F_3 results confirmed the assumption of the presence of a dominant inhibiting factor and two dominant factors for dwarfness.

Studies were also made in the inheritance of chaff colour in two of the crosses. In each case a single factor determined the inheritance of this characteristic. Correlation studies indicated the independent inheritance of chaff colour and bunt resistance in this cross.

The writer acknowledges valuable suggestions and help from Dr. W. L. Waterhouse, University of Sydney, and assistance supplied by the Principal and staff of the Hawkesbury Agricultural College, Richmond, N.S.W.

Bibliography.

Biffen, R. H., 1905.—Mendel's law of inheritance and wheat breeding. *Journ. Agr. Sci.*, Vol. 1, pp. 448.

————, 1907.—Studies in the Inheritance of Disease Resistance. *Journ. Agr. Sci.*, Vol. 2, Pt. 2, pp. 109-128.

Briggs, F. N., 1926.—Inheritance of Resistance to Bunt, *Tilletia tritici* in wheat. *J.A.R.*, Vol. 32, No. 10, pp. 973-990.

————, 1929*a*.—Inheritance of the Second Factor for Resistance to Bunt. *Tilletia tritici* in Hussar wheat. *J.A.R.*, Vol. 40, No. 3, pp. 225-232.

————, 1929*b*.—Inheritance of Resistance to Bunt. *Tilletia tritici* in White Odessa wheat. *J.A.R.*, Vol. 40, No. 4, pp. 353-359.

————, 1929*c*.—Factors which modify the resistance of Wheat to Bunt. *Tilletia tritici*. *Hilgardia*, Vol. 4, No. 7, pp. 175-184.

————, 1931.—Inheritance to Bunt, *Tilletia tritici* in hybrids of White Federation and Banner Berkeley Wheats. *J.A.R.*, Vol. 42, No. 5, pp. 307-313.

Churchward, J. G., 1931.—Studies in the Inheritance of Resistance to Bunt in a cross between Florence and Hard Federation wheats. *Proc. Roy. Soc. N.S.W.*, Vol. 64, pp. 298-319.

Forster, H. C., and Vasey, A. J., 1931.—Investigations on yield in cereals, Victoria, I. Census Studies, 1927-1929. *Journ. Agr. Sci.*, Vol. 21, Pt. 2, pp. 391-409.

Farrer, W., 1901.—Results of the Lambrigg Bunt Experiments of 1900. *Agric. Gazette N.S.W.*, Vol. 12, p. 419.

Gaines, E. F., 1920.—The Inheritance of Resistance to Bunt or Stinking Smut of wheat. *Journ. Amer. Soc. Agron.*, Vol. 12, No. 4, pp. 124-131.

————, 1923.—Genetics of Bunt Resistance in Wheat. *J.A.R.*, Vol. 23, pp. 445-480.

————, 1925.—The Inheritance of Disease Resistance in Wheat and Oats. *Phytopath.*, Vol. 15, No. 6, pp. 341-351.

GAINES, E. F., and SINGLETON, H. P., 1926.—Genetics of Marquis × Turkey wheat in respect to Bunt Resistance, Winter habit and awnlessness. *J.A.R.*, Vol. 32, No. 2, pp. 165-181.

HAYES, H. K., and GARBER, R. J., 1927.—Breeding Crop Plants, New York. McGraw-Hill Book Company.

KEZER, ALVIN, and BREEZE BOYACK, 1918.—Mendelian inheritance in wheat and barley crosses. *Colo. Agr. Exp. Sta.*, Bull. 249.

LOVE, H. H., and CRAIG, W. T., 1918.—Methods used and results obtained in Cereal investigations at the Cornell Station. *Journ. Amer. Soc. Agron.*, Vol. 10, pp. 145-157.

PERCIVAL, JOHN, 1921.—The Wheat Plant—A Monograph. London: Duckworth & Co., pp. 68-70.

PYE, H., 1909.—Diseases and Pests of Cereals. *Journ. Dept. Agr. Victoria*, Vol. 7, pp. 368-373.

WALDRON, L. R., 1924.—A Study of Dwarfness in wheat accompanied by Unexpected Ratios. *Genetics*, 9, pp. 212-246.

WATERHOUSE, W. L., 1930.—Australian Rust Studies. III. PROC. LINN. SOC. N.S.W., 55, Pt. 5, pp. 596-636.